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RESEARCH ARTICLE

Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers

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Abstract

Flow regulation via impoundments threatens lotic ecosystems and the services they provide globally. Impoundments drastically alter flow and stream temperature variability within fluvial environments, but efforts to quantify ecohydrological and ecothermal responses to flow regulation in conjunction have been sparsely explored to date. This study examined macroinvertebrate community responses to antecedent flow (discharge) and stream temperature variability across paired regulated and non-regulated systems associated with three reservoirs located in adjacent catchments. Community abundances, functional traits, and biomonitoring indices were examined, and ecological differences between non-regulated and regulated sites were quantified, with the most sensitive faunal response being correlated against a suite of flow and thermal indices. Regulated sites exhibited reduced low-flow variability and rapid increases in discharge during peak flows that regularly exceeded those conveyed by non-regulated sites, while stream temperature variability was highly congruent between sites. Macroinvertebrate functional traits were particularly sensitive to flow regulation, and incorporating biomonitoring indices marginally improved the ecological discrimination between regulated and non-regulated sites. Unlike community abundances, functional traits did not vary spatially between catchments, highlighting that such information could guide the implementation of regional environmental flows. Macroinvertebrate communities responded significantly to various hydrological parameters, particularly those associated with the timing of extreme flows, but were less sensitive to thermal controls. Future research should explore ecological responses to antecedent hydrological and stream temperature variability associated with flow regulation to provide a better understanding of the underlying mechanisms driving biotic alterations, which could guide future environmental flow methodologies.

KEYWORDS

environmental flows, hydrology, impoundment, invertebrate, thermal

1 | INTRODUCTION

Hydrological modifications to the natural flow regime via river regulation (Richter, Baumgartner, Powell, & Braun, 1996; Armanini *et al.*, 2014) and particularly impoundment threaten the integrity of fluvial ecosystems globally (Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff & Zimmerman, 2010; Cortez, Growns, Mitrovic, & Lim, 2012; Gillespie,

Desmet, Kay, Tillotson, & Brown, 2015b). The construction of impoundments disrupts the longitudinal continuity of fluvial ecosystems, as illustrated by the "Serial Discontinuity Concept" (*sensu* Ward & Stanford, 1983). Such barriers often compromise the biotic integrity of rivers by restricting the downstream transport of sediments and trophic resources (Growns & Growns, 2001; Katano *et al.*, 2009), as well as the migration of lotic fauna including iconic fish populations

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(Pelicice, Pompeu, & Agostinho, 2015) and other taxa such as macroinvertebrates (Satake & Ueno, 2012). In addition, river regulation modifies downstream channel morphologies (Carling, 1988; Petts & Gurnell, 2005) and the physico-chemical properties of impounded waters and their tailwaters, including dissolved oxygen (Nürnberg, 2002; Satake & Ueno, 2012) and stream temperature variability (Webb & Walling, 1996; Casado, Hannah, Peiry, & Campo, 2013). Such modifications have potentially significant ecological implications (see Ward & Stanford, 1983, 1995; Ellis & Jones, 2013), although the number of studies quantifying the long-term biotic responses to multiple environmental variables modified by flow regulation has been limited. Hydrological and thermal modifications downstream of impoundments have been found to persist over greater longitudinal distances compared to other environmental variables, such as periphyton concentration and substrate composition (Ellis & Jones, 2014). As such, quantifying ecological responses to flow and stream temperature variability across multiple years would allow key drivers of biotic change to be observed and quantified on an interannual basis, which could underpin the development of future “environmental flow” strategies (Olden & Naiman, 2010; Acreman *et al.*, 2014; Gillespie *et al.*, 2015b; King *et al.*, 2015).

Environmental flows (e-flows) refer to the sustainable delivery of water capable of supporting aquatic ecosystems and the services they provide (Arthington, Naiman, McClain, & Nilsson, 2010; Acreman *et al.*, 2014). Approaches to e-flows associated with impoundments have been historically centered on sustaining a minimum flow that is capable of supporting a target species (Petts, 2009). However, the development of the “Indicators of Hydrologic Alteration” (*sensu* Richter *et al.*, 1996) and the “Range of Variability Approach” (*sensu* Richter, Baumgartner, Wigington, & Braun, 1997) prompted the development of novel methods for quantifying hydrological modifications induced by anthropogenic activities (such as river regulation) centered around the five facets of the natural flow regime: “magnitude,” “frequency,” “duration,” “timing,” and “rate of change” (Poff *et al.*, 1997). Such frameworks have underpinned the identification and examination of over 200 “ecologically relevant” flow indices (Olden & Poff, 2003; Monk, Wood, Hannah, & Wilson, 2007) that have been related to ecological responses in lotic environments across a wide range of studies (e.g., Englund & Malmqvist, 1996; Clausen & Biggs, 1997; Monk *et al.*, 2006; Kennen, Riva-Murray, & Beaulieu, 2010; Belmar *et al.*, 2013; Worrall *et al.*, 2014). Such ecohydrological relationships have also been established to quantify the biotic alterations driven by different forms of hydrological modification, including river impoundments (Armanini *et al.*, 2014) and groundwater abstraction (Kennen, Riskin, & Charles, 2014).

Although there has been a historical emphasis on the volume of water available to the environment, there is increasing acknowledgement that e-flow methodologies should also consider stream temperature variability within lotic systems (e.g., Olden & Naiman, 2010). Recent research has illustrated this through the exploration of stream temperature variability occurring across the five facets that comprise the natural flow regime (Chu, Jones, & Allin, 2010; Casado *et al.*, 2013), implying that both thermal and hydrological indices share significant ecological relevance. Considering and quantifying ecological responses to flow and stream temperature variability in unison have

the potential to provide a greater understanding of what mechanisms are driving instream community responses to river regulation and a platform for guiding the development of e-flow frameworks, which has seldom been explored to date (but see Jackson, Gibbins, & Soulsby, 2007).

The functional traits (biological properties and ecological preferences) of macroinvertebrate communities are being increasingly utilized by scientists and practitioners to provide a greater causal understanding of biotic responses to a range of anthropogenic stressors (see Statzner & Bêche, 2010), including hydrological alterations (Tupinambás *et al.*, 2014; Dolédec *et al.*, 2015). However, the examination of taxonomic compositions may provide additional insights into how individual taxa respond to hydrological modifications, including non-native organisms that frequently proliferate in systems with modified flow regimes (Bunn & Arthington, 2002). In addition, a number of routine biomonitoring indices based on faunal preferences and tolerance ranges to different environmental parameters have been used to quantify macroinvertebrate community responses to flow regulation (e.g., Armanini *et al.*, 2014; Gillespie, Brown, & Kay, 2015a). Evidently, ecological information can be processed in various forms, but these may not respond consistently to the construction of impoundments and few studies have quantified their relative sensitivity to flow regulation (but see Tupinambás *et al.*, 2014).

This paper examines medium-term ecological responses to antecedent flow and stream temperature variability across paired regulated and non-regulated (control) sites associated with three reservoirs. The study aims are threefold: (a) to assess how reservoirs with comparable operational regimes influence stream temperature and flow (discharge) variability; (b) to examine how impoundments have modified the macroinvertebrate communities (community abundances, functional traits, and biomonitoring indices) compared to adjacent non-regulated sampling sites; and (c) to quantify macroinvertebrate responses to flow and stream temperature variability across paired regulated and non-regulated sampling sites over multiple years.

2 | METHODS

2.1 | Study area

Six sampling sites were examined across three impoundments (Clatworthy, Durleigh, and Sutton Bingham reservoirs) within the county of Somerset, UK (Figure 1) across the study period (2003–2011). Paired non-regulated and regulated sampling sites were located <2 km upstream and downstream of the impounding structures, respectively. The reservoirs studied displayed differing trophic statuses and physical properties (Table 1) but were selected for comparison due to (a) their geographical proximity within the same region (all sites experience a comparable climate, overlay similar geologies, and are operated by Wessex Water plc.); (b) the availability of ecological (macroinvertebrate) and antecedent abiotic (flow and stream temperature) information from the same sampling sites across multiple years; and (c) all reservoirs being subject to comparable reservoir operational regimes. Each impoundment releases a continuous compensation flow downstream and all possess a spill weir that facilitate rapid increases in discharge downstream when water levels reach maximum capacity.

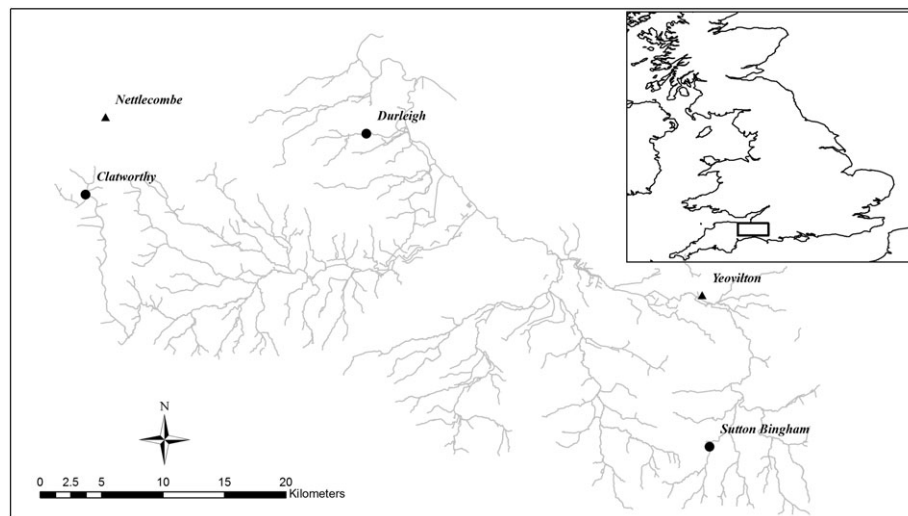


FIGURE 1 Reservoirs (circles) studied across Somerset and BADC air stations (triangles)

TABLE 1 Environmental characteristics of the reservoirs examined in this study

Reservoir	Trophic state*	Altitude (m aod)	Max depth (m)	Area (km ²)
Clatworthy	Mesotrophic (26.1)	255	29.3	0.49
Sutton Bingham	Eutrophic (94.97)	20	12.2	0.53
Durleigh	Hyper-eutrophic (466.13)	53	7.9	0.33

*Average total phosphorus ($\mu\text{g l}^{-1}$) between 2005 and 2011. N.B. Classification based on OECD (1982).

In addition, all of the reservoirs operate continuous aeration systems that prevent thermal stratification throughout the year.

2.2 | Flow and temperature data

Hydrological variability at regulated sampling sites was measured by gauges at each of the reservoir outflows that provided average daily discharge values (m^3/s). Flows at all non-regulated sampling sites were derived via hydrological models (mass-balance or area-runoff) developed by the regional water company (Wessex Water plc.). The models output an average weekly discharge value (m^3/s) and have been approved as accurate representations of non-regulated flows by the Environment Agency (EA—the statutory environmental regulator in England; Wessex Water, 2013). Stream temperature records were collected from each sampling site at 15-minute intervals using “Tinytag” temperature loggers for a minimum of 12 months between 2011 and 2012. For the purpose of extending stream temperature time-series across the study period, daily maximum air temperatures were obtained from the “British Atmospheric Data Centre” for Yeovilton and Nettlecombe weather stations (Figure 1), which were located within 25 km of the three impounding structures.

2.3 | Macroinvertebrate sampling

Macroinvertebrate samples were collected by the EA and Wessex Water as part of routine biomonitoring programs along the three watercourses (six sampling sites—paired non-regulated and regulated). All samples were collected using a standardized 3-min kick method, supplemented with a 1-min hand search following the standard procedure specified by the EA (Murray-Bligh, 1999). Macroinvertebrate

communities were subsequently identified to family-level, except for Hydracarina, Microtubellaria, Nematoda, Ostracoda, and Oligochaeta, which were identified as such. Ecological data included in this study were screened so that for a given year, only samples taken in both spring and autumn from respective pairs of non-regulated and regulated sampling sites were included for analysis ($n = 44$).

2.4 | Data analysis

The following section is subdivided into three parts to outline the analytical procedures used to address each of the study aims and is presented schematically in Figure 2.

2.4.1 | Flow and temperature regimes

Flow, air, and stream temperature time series were initially screened so that any missing values accounted for <10% of the total record (Monk *et al.*, 2006). Missing values were subsequently interpolated using the “na.approx” function within the “zoo” package (Zeileis, Grothendieck, Ryan, & Andrews, 2015) using R studio version 3.0.2 (R Development Core Team, 2014). The hydrological models used for non-regulated flows provide an average weekly discharge value. As such, gauged flow, air, and stream temperature time series were aggregated to average weekly values to ensure equivalent temporal resolutions were used for all hydrological and thermal datasets. Air temperatures were converted using the environmental lapse rate to account for differences in sampling site altitudes following the approach outlined in Durand and Ormerod (2007). These were subsequently modeled against stream temperatures, whereby nonlinear relationships were evident due to asymptotic relationships arising at extreme

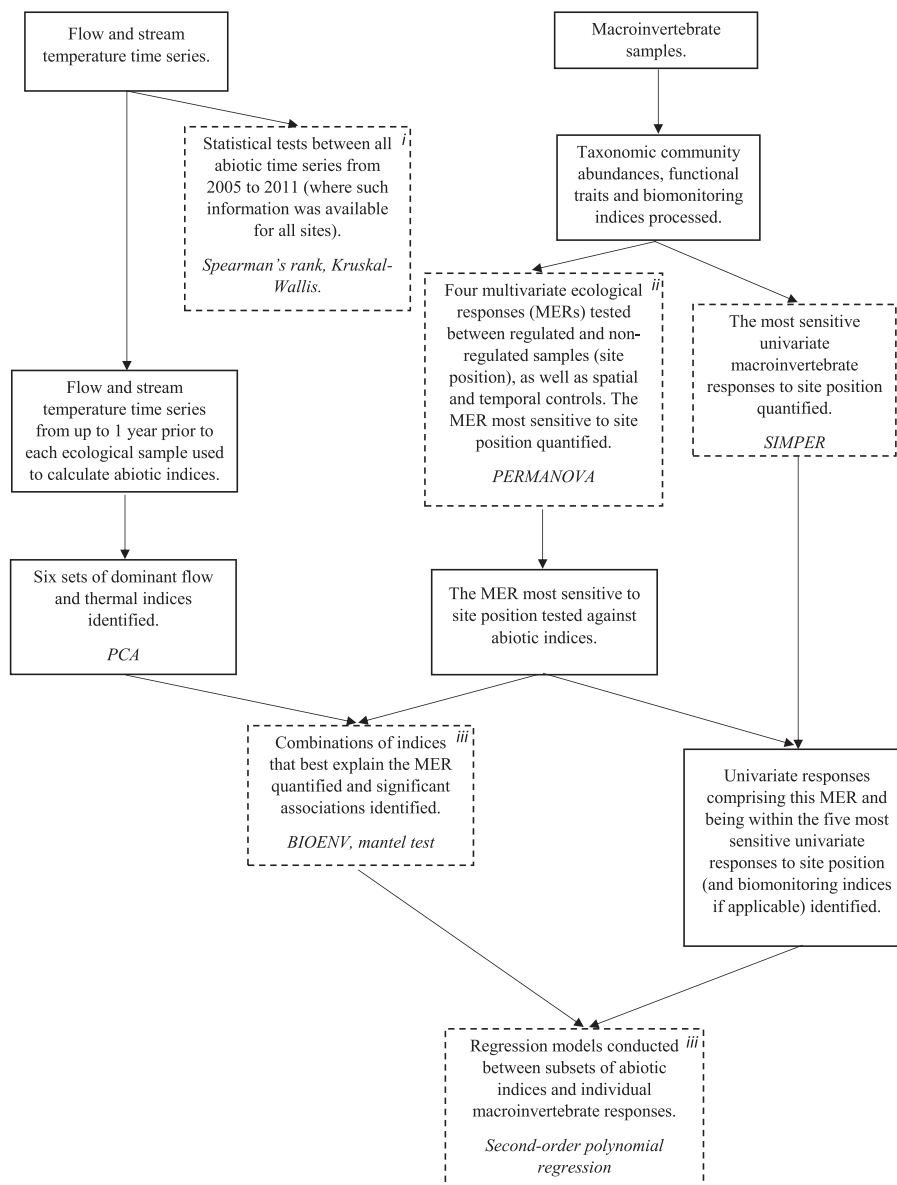


FIGURE 2 A flow chart depicting the analytical framework adopted within this study. Rectangles with dashed lines represent outputs corresponding to each of the specific study aims. Italicized text represents the statistical techniques used

temperatures (see Mohseni & Stefan, 1999). As such, “Generalized Additive Models” were constructed between air and stream temperatures within the “mgcv” package in R studio (Wood, 2015). These models accounted for 91.6–96.6% of the variation between air and stream temperature time series and were highly significant (all p -values $\leq 2 \times 10^{-16}$), which allowed stream temperature values to be reconstructed for all periods when air temperature data was available.

Although both flow and stream temperature time series were available across the whole study period for a subset of the six sampling sites, this abiotic information was only obtainable for all sampling sites between 2005 and 2011. As such, flow and stream temperature time series across this period were used as separate inputs to address the first aim of the study (see Figure 2), with quantile–quantile (QQ) plots highlighting non-normality when this abiotic information was inputted within linear models. Thus, a Spearman's rank correlation coefficient (r) was used as a measure of association between flow and stream temperature time series between all pair combinations of the six sampling

sites. Statistical differences between flow and stream temperature time series exhibited by regulated and non-regulated sampling sites were examined using a Kruskal–Wallis test (a non-parametric one-way analysis of variance), using “site position” (i.e., upstream–non-regulated and downstream–regulated) as a primary factor.

2.4.2 | Ecological responses

Relative community abundances (“relative” due to kick samples representing a semi-quantitative approach), functional traits, and biotic indices (denoting the extent of different abiotic stressors based on faunal communities) of macroinvertebrate samples were explored in relation to flow regulation. The nomenclature of functional traits is reported herein by their “grouping features” and “traits” (see Schmera, Podani, Heino, Erős, & Poff, 2015). Grouping features represent a functional trait category (e.g., “maximum body size” and “feeding groups”), while traits signify modalities residing within these (e.g., maximum body size—“ ≤ 0.25 cm,”

" ≥ 8 cm"; feeding groups—"filter-feeder," "predator"). Macroinvertebrate functional traits were processed from a database initially developed in France, which possesses trait information typically available at species or genus level (Tachet, Bournaud, Richoux, & Usseglio-Polatera, 2010). This database utilizes a "fuzzy-coding" approach, whereby macroinvertebrate affinities for individual traits range from zero (indicating no affinity) to three or five (indicating strong affinity—the maximum value depending on the level of information available in existing literature—see Chevene, Dolédec, & Chessel, 1994; Tachet *et al.*, 2010). Prior to the processing of functional traits, specialist freshwater macroinvertebrate ecologists across various academic and industrial institutions within the UK were consulted to provide their expert input on utilizing the traits database within the context of this research (full details of this procedure are summarized in Appendix A).

Following consultation with national experts, a total of 12 grouping features comprising 82 traits were utilized from the functional traits database in subsequent analyses (Table 2). The processing of functional traits initially involved removing taxa that do not occur within the UK (guided by Davies & Edwards, 2011) from the database (*sensu* Demars, Kemp, Friberg, Usseglio-Polatera, & Harper, 2012), as well as those not sampled within this study. In addition, Chironomidae and all specimens recorded at a taxonomic resolution coarser than family-level were excluded (as suggested by freshwater macroinvertebrate specialists consulted during the development process) due to high species diversity within these taxonomic groups. Trait values were then standardized so that each grouping feature summed to 1. Subsequently, each genus/species examined within the traits database (i.e., those comprising families observed within this study) was weighted by a proportional likelihood of occurrence (as suggested by freshwater macroinvertebrate specialists). This was based on 61 macroinvertebrate samples (identified predominantly to species-level and used only to facilitate a weighted family average within this study) collected as part of routine biomonitoring from both regulated and non-regulated watercourses across the study area (see Appendix A). For this, trait values were multiplied by the percentage of samples that each genus/species was found within out of the 61 samples from the species-level dataset. This allowed abundant taxa in lotic environments across the region to be given a higher weighted influence. Family-averaged trait values were calculated and then standardized (as above) to account for taxa expressing no affinity for all traits within a specific grouping feature. Subsequently, a trait by taxonomic abundance array was created by multiplying trait values by $\ln(x + 1)$ transformed taxonomic community abundances, each trait was averaged across all taxa and standardized (as above) to account for differences in abundances between sites (Gayraud *et al.*, 2003).

Three biomonitoring indices used widely in the UK were explored to summarize the ecological sensitivity of macroinvertebrate communities to abiotic variables potentially influenced by flow regulation. Specifically, the "Lotic-invertebrate Index of Flow Evaluation" (LIFE—Extence, Balbi, & Chadd, 1999); the "Proportion of Sediment-sensitive Invertebrates" (PSI—Extence *et al.*, 2013); and the "Average Score per Taxon" (ASPT—a temporally robust derivative of the "Biological Monitoring Working Party" score—Armitage, Moss, Wright, & Furze, 1983) were used to explore the structure of macroinvertebrate communities based on flow (discharge), substrate composition, and the trophic status, respectively.

To examine the most sensitive taxa and traits (univariate responses) to flow regulation, similarity percentages (SIMPER) analysis was implemented using regulated versus non-regulated sites ("site position" herein) as a primary factor (see Figure 2). Its significance was tested using 999 permutations within the "Vegan" software package (Oksanen *et al.*, 2016). This procedure was also undertaken for biomonitoring indices to comparatively quantify the sensitivity of these community metrics to flow regulation.

Four matrices comprising representations of different macroinvertebrate compositions were explored via multivariate analyses to quantify the sensitivity of each of these "multivariate ecological responses" (MERs) to flow regulation, as well as spatial and temporal variability (see Figure 2): (a) relative community abundances—"taxonomic"; (b) functional traits comprising only biological properties (see Table 2)—"biological traits"; (c) functional traits from all 12 grouping features—"all functional traits"; and (d) "functional traits and biomonitoring indices." The latter comprised the same inputs as "all functional traits" but with LIFE, PSI, and ASPT scores replacing all traits within the "velocity," "substrate," and "trophic status" grouping features from the functional trait database, respectively. All values within the "taxonomic" MER were $\ln(x + 1)$ transformed to reduce the influence of abundant taxa, while all other MERs were standardized by dividing values by the standard deviation of each variable (but not centralized as conducted with z-scores to avoid negative values), thus ensuring comparability between different responses.

Non-metric multidimensional scaling (NMDS) was used to visualize differences of MERs between each "site position" (i.e. regulated and non-regulated) using the "metaMDS" function within Vegan. Differences in MERs were quantitatively explored in relation to flow regulation, as well as spatial and temporal controls, with the additive effects of "site position," "reservoir" (separate river systems hosting each impoundment), "season," and "year" being tested within a permutational multivariate analysis of variance (PERMANOVA) via the "adonis" function within the Vegan package (it should be noted alternative forms of PERMANOVA, including nested designs and interactive effects, were also conducted and are summarized in Appendix B). The variance explained by site position within the PERMANOVA for each MER, as well as the aforementioned SIMPER analysis, was used to guide which ecological responses were to be included in the following analyses (see Figure 2).

2.4.3 | Ecohydrological and ecothermal analysis

Two hundred and twenty-four abiotic indices (114 flow and 110 thermal) based around the five facets of the natural flow regime identified in previous studies (Olden & Poff, 2003; Monk *et al.*, 2007—see Appendix C, Table C1) were calculated and used to summarize the antecedent flow and stream temperature variability exposed to macroinvertebrate communities. These were derived from flow and stream temperature time series from up to 1 year prior to the date of each macroinvertebrate sample collection. Fifty dominant flow and thermal indices were identified through a principal component analysis (PCA) following the procedure outlined by Olden and Poff (2003), thus minimizing redundancy between abiotic indices and identifying the major sources statistical variation. This reduced set of indices was examined in a Pearson-product moment correlation matrix, and

TABLE 2 Macroinvertebrate functional traits examined within this study, with biological traits in non-italicized text and ecological traits being italicized

Grouping feature	Trait	Code	Grouping feature	Trait	Code
Maximum potential size	≤0.25 cm	Size.1	Respiration method	Gill	Respiration.1
	>0.25–0.5 cm	Size.2		Plastron	Respiration.2
	>0.5–1 cm	Size.3		Spiracle	Respiration.3
	>1–2 cm	Size.4		Hydrostatic vesicle	Respiration.4
	>2–4 cm	Size.5		Tegument	Respiration.5
	>4–8 cm	Size.6	Food consumed	Microorganisms	Food.1
	>8 cm	Size.7		Detritus <1 mm	Food.2
Life cycle duration	≤1 year	Life-cycle.1		Dead plant ≥1 mm	Food.3
	>1 year	Life-cycle.2		Living microphytes	Food.4
Voltinism	<1	Voltinism.1		Living macrophytes	Food.5
	1	Voltinism.2		Dead animal ≥1 mm	Food.6
	>1	Voltinism.3		Living macroinvertebrates	Food.7
Aquatic stages	Egg	Stage.1		Living macroinvertebrates	Food.8
	Larva	Stage.2		Vertebrates	Food.9
	Nymph	Stage.3	Feeding group	Absorber	Feeding.1
	Adult	Stage.4		Deposit feeder	Feeding.2
Reproduction strategy	Ovoviviparity	Reproduction.1		Shredder	Feeding.3
	Isolated, free eggs	Reproduction.2		Scraper	Feeding.4
	Isolated, cemented eggs	Reproduction.3		Filter-feeder	Feeding.5
	Clutches, cemented	Reproduction.4		Piercer	Feeding.6
	Clutches, free	Reproduction.5		Predator	Feeding.7
	Clutches, in vegetation	Reproduction.6		Parasite	Feeding.8
	Clutches, terrestrial	Reproduction.7			
	Asexual	Reproduction.8	<i>Substrate preference</i>	<i>Coarse substrates</i>	<i>Substrate.1</i>
Dispersal strategy	Aquatic passive	Dispersal.1		<i>Gravel</i>	<i>Substrate.2</i>
	Aquatic active	Dispersal.2		<i>Sand</i>	<i>Substrate.3</i>
	Aerial passive	Dispersal.3		<i>Silt</i>	<i>Substrate.4</i>
	Aerial active	Dispersal.4		<i>Macrophytes</i>	<i>Substrate.5</i>
Resistance form	Eggs/statoblasts	Resistance.1		<i>Microphytes</i>	<i>Substrate.6</i>
	Cocoons	Resistance.2		<i>Twigs/roots</i>	<i>Substrate.7</i>
	Housings against desiccation	Resistance.3		<i>Organic detritus</i>	<i>Substrate.8</i>
	Diapause / dormancy	Resistance.4		<i>Mud</i>	<i>Substrate.9</i>
	None	Resistance.5	<i>Velocity preference</i>	<i>Null</i>	<i>Velocity.1</i>
Locomotion and substrate relation	Flier	Locomotion.1		<i>Slow</i>	<i>Velocity.2</i>
	Surface swimmer	Locomotion.2		<i>Medium</i>	<i>Velocity.3</i>
	Full water swimmer	Locomotion.3		<i>Fast</i>	<i>Velocity.4</i>
	Crawler	Locomotion.4	<i>Trophic status</i>	<i>Oligotrophic</i>	<i>Trophic.1</i>
	Burrower	Locomotion.5		<i>Mesotrophic</i>	<i>Trophic.2</i>
	Interstitial	Locomotion.6		<i>Eutrophic</i>	<i>Trophic.3</i>
	Temporarily attached	Locomotion.7	<i>Thermal tolerance</i>	<i>Psychrophilic</i>	<i>Thermal.1</i>
	Permanently attached	Locomotion.8		<i>Thermophilic</i>	<i>Thermal.2</i>
				<i>Eurythermic</i>	<i>Thermal.3</i>

indices possessing r values greater than 0.95 were removed, which was necessary where “perfect collinearity” (which occurs where variables are calculated from the same parameters) existed. Subsequently, abiotic indices were iteratively removed until all “Variance Inflation Factor” values were below 3 to avoid collinearity between these explanatory variables (Zuur, Ieno, & Elphick, 2010). Dominant flow and thermal indices were obtained separately for regulated and non-regulated sites, as well as for both spring and autumn sampling

periods within each of these ‘site positions’, producing six sets of dominant abiotic indices.

Statistical outputs from the PERMANOVA were subsequently used to highlight which MER was most sensitive to flow regulation (see Figure 2). This was achieved by examining which MER exhibited the highest amount of ecological variance explained by site position. This MER was then correlated against each of the six groups of dominant abiotic indices using the “*bioenv*” function within Vegan. This statistical

technique highlighted different subsets of flow and thermal indices that best explained macroinvertebrate responses based on the rank correlation between the Euclidean distances of environmental variables and community (Bray–Curtis) dissimilarities (Oksanen *et al.*, 2016). The significance of the three models displaying the highest correlation for each of the six groups of dominant abiotic indices was determined via a “mantel” test within the Vegan package, with flow and thermal indices comprising significant associations being used within the subsequent univariate analyses (see Figure 2).

Abiotic indices comprising significant ecohydrological and ecothermal associations were used as explanatory variables within univariate regression analyses against a select number of individual macroinvertebrate responses. These response variables were selected based on two criteria: (a) they comprise the MER found to be most sensitive to site position (i.e., the MER used within ecohydrological and ecothermal associations, which was identified via PERMANOVA; see Figure 2) and (b) they were within the five traits or taxa (whichever is appropriate based on the aforementioned criteria—and additionally the three biomonitoring indices if applicable based on the previous criteria) most sensitive to site position, as indicated by the SIMPER analysis (*sensu* Brown & Milner, 2012; see Figure 2). Pairwise second-order polynomial regressions were subsequently fitted between all explanatory and response variables. This technique has been shown to reliably model nonlinear associations between macroinvertebrate responses and abiotic indices, without overfitting models (e.g., Kennen *et al.*, 2014). To account for large numbers of models being constructed, the significant α level was adjusted through an alternative to the Bonferroni correction, which multiplies the

degrees of freedom within the statistical models by 0.05, before dividing by the total number of tests (see Dolédec, Phillips, Scarsbrook, Riley, & Townsend, 2006—see Appendix B for statistical outputs obtained from all models used within this univariate analysis).

3 | RESULTS

3.1 | Flow and thermal regimes

Hydrological changes driven by impoundments were evident, with regulated sites experiencing reduced low flow variability and rapid increases in discharge peaks frequently surpassing those exhibited by non-regulated sites (Figure 3). Hydrological variability displayed a lower correlation between sites compared to thermal regimes (Table 3), reflecting the congruency of stream temperature patterns exhibited on an interannual basis compared to more spatially variable hydrological variability (Figure 3). However, differences in the magnitude of stream temperatures were evident, with regulated sites at Clatworthy and Durleigh reservoirs being on average 1.24°C (maximum weekly difference = +3.84°C) and 2.21°C (maximum weekly difference = +5.78°C) warmer than their paired non-regulated site, respectively. The regulated site at Sutton Bingham reservoir was on average 1.61°C colder (maximum weekly difference = −4.25°C) than its corresponding non-regulated site. Kruskal–Wallis tests highlighted that flow ($\chi^2 = 45.20$, p -value = 0.001) and stream temperature ($\chi^2 = 9.87$, p -value = 0.002) time series differed between site position (non-regulated versus regulated sites), with the former highlighting greater differences in flow variability

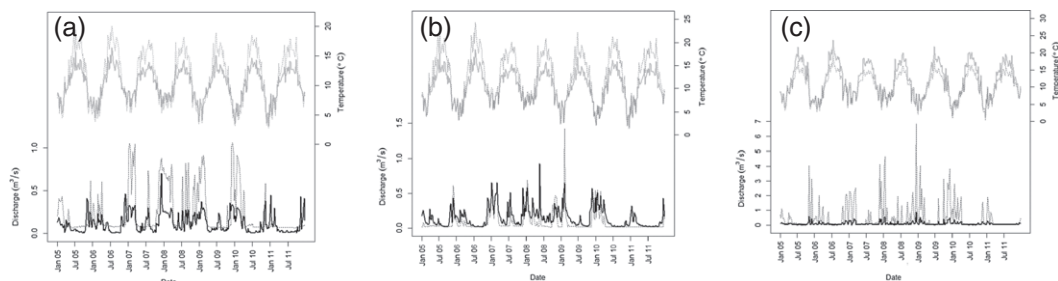


FIGURE 3 Flow (black) and thermal (gray) time-series at each reservoir at non-regulated (dashed line) and regulated (solid line) sites for (a) Clatworthy, (b) Durleigh, and (c) Sutton Bingham

TABLE 3 Spearman's rank correlation between flow (non-italicized) and thermal (italicized) time series

		Clatworthy upstream	Clatworthy downstream	Durleigh upstream	Durleigh downstream	Sutton Bingham upstream	Sutton Bingham downstream
		<i>Temperature</i>					
Clatworthy upstream	Flow	-	1.00	1.00	1.00	0.97	0.97
Clatworthy downstream		0.69	-	1.00	1.00	0.97	0.97
Durleigh upstream		0.78	0.69	-	1.00	0.97	0.97
Durleigh downstream		0.43	0.78	0.63	-	0.97	0.97
Sutton Bingham upstream		0.77	0.43	0.74	0.40	-	1.00
Sutton Bingham downstream		0.67	0.77	0.67	0.53	0.76	-

between regulated and non-regulated sites compared to thermal variability (as it possesses a much greater X^2 value).

3.2 | Ecological responses

SIMPER analysis highlighted a range of macroinvertebrate families (spanning across several taxonomic orders) differed significantly between each site position, with many increasing in relative abundance within regulated systems (Table 4). Similarly, a range of traits from several grouping features differed significantly between each site position, with traits related to faunal life histories and feeding strategies responding most frequently relative to those comprising other grouping features (Table 4). However, the number of trait responses displaying greater affinities for regulated sites was more varied than those for individual taxa. All biomonitoring indices differed significantly between regulated and non-regulated sampling sites (Table 4).

TABLE 4 SIMPER analysis of univariate macroinvertebrate responses most sensitive to flow regulation: * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; NS = non-significant. (a) Individual taxa; (b) Individual traits, and (c) Biomonitoring indices

Univariate response		Average non-regulated	Average regulated
a)	Hydropsychidae***	1.05	5.86
	Asellidae***	0.53	4.42
	Sphaeriidae***	1.93	4.86
	Heptageniidae***	3.47	0.66
	Caenidae***	0.43	3.10
	Planariidae***	0.72	3.11
	Baetidae**	4.62	2.74
	Tipulidae***	2.70	0.37
	Erpobdellidae***	0.26	2.40
	Gammaridae (NS)	3.54	2.84
b)	Reproduction.3***	0.24	0.10
	Feeding.4***	0.32	0.19
	Trophic.1***	0.41	0.29
	Velocity.1***	0.15	0.27
	Reproduction.4***	0.42	0.53
	Food.8***	0.10	0.21
	Feeding.7***	0.10	0.21
	Stage.4***	0.10	0.19
	Velocity.3***	0.35	0.27
	Dispersal.4***	0.26	0.18
c)	PSI***	66.65	37.01
	ASPT***	6.68	5.36
	LIFE***	7.59	6.48

PERMANOVA indicated that macroinvertebrate communities were relatively insensitive to temporal variability, with no MER differing significantly between seasons and years, while the "taxonomic" MER was the only macroinvertebrate response to differ significantly between watercourses (Table 5). PERMANOVA highlighted that all MERs were significantly different between site position, with "functional traits and biomonitoring indices" accounting for the greatest amount of ecological variance, but this only varied by 5% across all MERs ($r^2 = 0.36$ – 0.41 ; Table 5). The NMDS procedure highlighted that all MERs possessed contrasting communities between regulated and non-regulated sampling sites (e.g., Figure 4).

3.3 | Ecohydrological and ecothermal associations

Relating "functional traits and biomonitoring indices" (the MER most sensitive between site position—Table 5) to abiotic parameters indicated that macroinvertebrate community responses were most highly correlated with 16 abiotic indices (14 flow and 2 thermal), with significant associations existing across all six groups of dominant abiotic indices (Table 6). All non-regulated samples displayed one significant association with a single hydrological index that yielded a weak correlation (QNCRR— $r = 0.22$). In contrast, all regulated samples possessed multiple significant associations that displayed higher correlations ($r = 0.38$ – 0.39) with up to five flow and thermal indices (Table 6). Ecohydrological associations typically displayed higher correlations when each season (spring and autumn) was examined individually ($r = 0.31$ – 0.60) and comprised only flow indices in all instances (Table 6). For the univariate analyses, second-order polynomial regressions were constructed between 16 abiotic indices and 8 univariate ecological responses (five traits most sensitive to flow regulation and three biomonitoring indices) and highlighted that the majority of univariate ecological responses were not significantly associated with dominant abiotic indices (see Appendix B). No flow or thermal index displayed a significant association with an ecological parameter across both regulated and non-regulated sites, while a moderate number ($n = 23$) displayed significant associations within regulated sites (e.g., Figure 5) compared to non-regulated sites ($n = 7$).

4 | DISCUSSION

4.1 | Flow regulation influences on hydrological and stream temperature variability

Our findings demonstrate that hydrological variability differed more profoundly between regulated and non-regulated sites than stream

TABLE 5 Importance of different environmental controls on various macroinvertebrate responses: NS = non-significant statistical models

Response variables	Site position		Reservoir		Season		Year	
	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value
Taxonomic	0.36	0.001	0.06	0.026	0.04	0.140(NS)	0.04	0.116(NS)
Biological traits	0.40	0.001	0.04	0.120 (NS)	0.02	0.395(NS)	0.04	0.131(NS)
All functional traits	0.40	0.001	0.06	0.055(NS)	0.02	0.395(NS)	0.04	0.103(NS)
Functional traits and biomonitoring indices	0.41	0.001	0.04	0.096(NS)	0.02	0.388(NS)	0.04	0.143(NS)

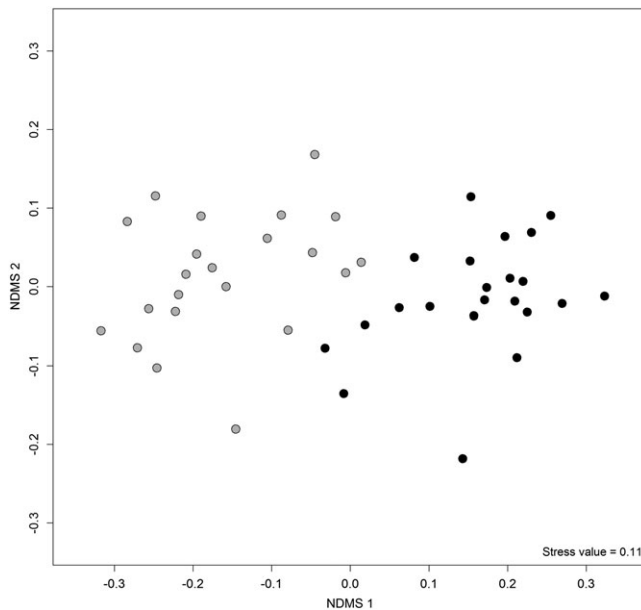


FIGURE 4 NMDS plot for regulated and non-regulated samples across all sites for functional traits and biomonitoring indices. Grey circles = non-regulated sites and black circles = regulated sites

temperatures. Congruent patterns of stream temperature variability between all sites were likely due to the geographical proximity of reservoirs (meaning they are exposed to comparable climatic regimes) and the use of aeration systems that prevented thermal stratification within impounded waters. This reservoir water mixing technique has been recommended as an effective way of mitigating ecological changes driven by thermal alterations within reservoirs (Olden & Naiman, 2010; Miles & West, 2011). However, stream temperatures across paired non-regulated and regulated sites consistently displayed differences in magnitude that ranged from an average of -1.61 to $+2.21^{\circ}\text{C}$. Thermal changes and differences of such magnitudes may be sufficient to drive ecological changes (e.g., Daufresne, Roger, Capra, & Lamouroux, 2004; Durance & Ormerod, 2007). In addition, maximum weekly differences between paired non-regulated and regulated sites

ranged by $>10^{\circ}\text{C}$ between reservoirs, with greater extremes likely to drive ecological change, particularly if the thermal tolerances of aquatic organisms are exceeded (Elliott & Elliott, 2010; Worthington, Shaw, Daffern, & Langford, 2015). This suggests that e-flow methodologies aiming to mitigate thermal regime modifications driven by impoundments need to incorporate combinative measures of “within-reservoir” techniques (see Olden & Naiman, 2010) and localized stream-based methods, such as altering the degree of riparian shading to offset alterations to the magnitude of thermal regimes (Hannah, Malcolm, Soulsby, & Youngson, 2008; Garner, Malcolm, Sadler, & Hannah, 2014; Johnson & Wilby, 2015).

The regulated sites examined in this study displayed reduced hydrological variability during periods of low flow and rapid rises in discharge during periods of elevated flows compared to non-regulated systems. As such, management strategies aiming to reinstate more “natural” flow regimes downstream of the impoundments would require more flexible compensation releases at low flows and water levels within reservoirs to be managed in a way that could hold back larger quantities of water during peak discharges. However, logistical and economic constraints may prevent the implementation of such water management strategies (Acreman *et al.*, 2009), and e-flow frameworks involving the management of specific flow releases based on key hydrological dependencies that lotic ecosystems require (e.g., the building block methodology—see King, Brown & Sabet, 2003; the functional flows approach—see Yarnell *et al.*, 2015) may provide a more pragmatic solution (Acreman *et al.*, 2009). However, such strategies are often hindered by limited knowledge of the nature of the “building blocks” required (Acreman *et al.*, 2014), and modeling biotic responses to hydrological variability could underpin such strategies, as proposed within the “Ecological Limits of Hydrological Alteration” (ELOHA) framework (Poff *et al.*, 2010) and conducted within this study.

4.2 | The sensitivity of different ecological responses to flow regulation

This study recorded various univariate ecological contrasts between non-regulated and regulated systems. Several macroinvertebrate

TABLE 6 Subsets of abiotic indices that possess the highest rank correlation between dominant abiotic indices and community dissimilarities: * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; NS = non-significant statistical models

Model	Abiotic indices	r
All non-regulated samples	QNCRR	0.22*
	QNCRR, TDAYMIN35	0.12 (NS)
	QNCRR, QPORR, TDAYMIN35	0.10 (NS)
All regulated samples	QCVANNMAX, QSEPMIN, QPORR, TDAYMAX91	0.39***
	QCVANNMAX, QSEPMIN, TDAYMAX91	0.39**
	QCVANNMAX, QSEPMIN, QPORR, TDAYMAX91, TNERR	0.38**
Spring non-regulated samples	QJUNMIN, QSTDMAXJW, QSTDMINJW	0.42**
	QJUNMIN, QSTDMAXJW	0.38*
	QJUNMIN	0.36*
Spring regulated samples	QJULMIN, QMEPOS	0.42**
	QJULMIN	0.39*
	QJULMIN, QD35MAX50, QMEPOS	0.31*
Autumn non-regulated samples	QLPC, QD91MAX50	0.60***
	QLPC, QD91MAX50, QMAXJW	0.53**
	QLPC, QD91MAX50, QMAXJW, QMEMAXJW	0.45**
Autumn regulated samples	QJUNMIN	0.44**
	QCVANNMAX, QJUNMIN	0.35*
	QCVANNMAX, QJUNMIN, QMEMAXJW	0.25 (NS)

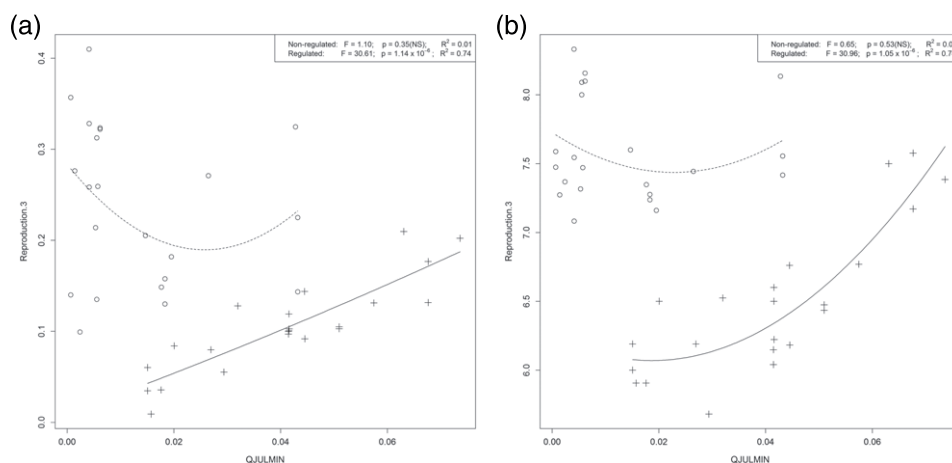


FIGURE 5 Scatterplots of univariate ecological responses to hydrological indices, with second-order polynomial regressions fitted and model summaries presented (NS = non-significant associations). Circles = non-regulated samples, crosses = regulated samples. Dashed line = non-regulated fitted model, solid line = regulated fitted model. (a) Fauna reproducing by laying isolated eggs down on the river bed against QJULMIN and (b) LIFE score against QJULMIN

families were found to increase in relative abundance at regulated sites, with the number of the caseless caddisfly larvae family Hydropsychidae increasing most markedly at downstream sites, while two Ephemeroptera families (Baetidae and Heptageniidae) displayed significant reductions. These findings are broadly in keeping with results recorded in previous research (e.g., Gillespie *et al.*, 2015a). Although a number of traits responded significantly to flow regulation, biological traits associated with life histories and feeding strategies were prominently affected. Tupinambás *et al.* (2014) not only found that comparable traits responded to hydro-peaking operations but also observed changes in faunal resistance strategies not recorded within this study, probably due to markedly different reservoir management operations. We found that biomonitoring indices reflecting ecological preferences for substrate composition, trophic status, and flow parameters differed significantly between non-regulated and regulated systems. This is in contrast to the findings of Gillespie *et al.* (2015a), who reported that the LIFE score responded negatively to regulation but that PSI and ASPT scores were largely unaffected. Moreover, our study found that incorporating biomonitoring indices within a multivariate context alongside functional traits resulted in a slightly higher proportion of ecological variance being accounted for between regulated and non-regulated systems. Incorporating such biomonitoring indices could therefore provide a more robust indication of community responses when considered alongside functional traits.

Macroinvertebrate functional traits have not been extensively utilized in aquatic ecological studies within the UK thus far (notable exceptions being Larsen & Ormerod, 2010; Demars *et al.*, 2012). Due to the functional traits database utilized in the present study being developed outside of the UK (although applicable to other European freshwater systems—Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000), incorporating expert knowledge of national specialists helped confirm the assignment of trait values (see Appendix A). We would strongly encourage future research utilizing macroinvertebrate functional traits from databases initially developed within alternative biogeographic regions to account for the opinions and recommendations of regional or national experts. This would help improve the

biological and ecological information underpinning functional traits across different study regions.

Functional traits are being increasingly used within aquatic ecological studies and provide various advantages compared to traditional taxonomic-based approaches including (a) spatially consistent ecological patterns, (b) enhanced statistical discrimination between tested environmental variables, and (c) a causal understanding of community responses to a wide range of parameters and stressors (see Menezes, Baird, & Soares, 2010; Statzner & Bêche, 2010). The results of this study supported such notions, with (a) different river systems supporting comparable trait compositions, (b) multivariate ecological responses comprising functional traits accounting for the greatest amount of ecological variance between non-regulated and regulated systems, and (c) individual (univariate) trait responses providing insights into the mechanisms underlying ecological responses to flow regulation. On the other hand, macroinvertebrate relative community abundances exhibited the weakest ecological discrimination between regulated and non-regulated sites (albeit minimally) and differed significantly between watercourses. This suggests that the utilization of functional traits may provide more robust river management solutions across wider geographical regions (Statzner & Bêche, 2010), highlighting how such information could underpin the implementation of regionally uniform e-flows, an integral component of the Ecological Limits of Hydrological Alterations framework (Poff *et al.*, 2010; see also Arthington, Bunn, Poff, & Naiman, 2006).

4.3 | Flow and thermal controls on macroinvertebrate communities

A number of studies have explored ecosystem responses to a suite of flow indices based around the five facets of the natural flow regime (e.g., Monk *et al.*, 2006; Belmar *et al.*, 2013; Kennen *et al.*, 2014). While there is increasing recognition that fluvial ecosystems respond to comparable forms of stream temperature variability (Olden & Naiman, 2010), few studies have explored the ecological implications of this,

and even less have examined biotic responses to flow and stream temperature variability together (a notable exception being Jackson *et al.*, 2007). Results from this study highlighted that macroinvertebrate communities from all non-regulated samples were weakly associated with a single flow parameter, suggesting that they may be sensitive to a wider range of environmental parameters (e.g., water quality or channel morphology), as reported by Worrall *et al.* (2014). Communities from regulated sites were significantly associated with antecedent maximum stream temperatures and a range of hydrological indices corresponding to different facets of the flow regime. The latter has been reported in previous studies centered on regulated watercourses (e.g., Englund & Malmqvist, 1996; Armanini *et al.*, 2014). However, macroinvertebrate communities being significantly associated with maximum stream temperatures within regulated systems contrasts to the results of previous studies highlighting ecological responses to colder stream temperatures caused by hypolimnetic flow releases into the tailwaters of impoundments (e.g., Phillips, Pollock, Bowman, MMaster, & Chivers, 2015). Webb and Walling (1996) conducted a detailed long-term study on stream temperature variability of sites upstream and downstream of a reservoir within southwest England (close to the area of this study) that also operates an aeration system to prevent thermal stratification. The authors recorded instances of warming within the regulated stream that was attributed to solar radiation heating the impounded surface area. Webb and Walling (1996) also described changes in stream temperatures ensuing from discharge variations downstream of the impoundment caused by compensation flow releases, springflow inputs, and the mixing of runoff sources. The association of faunal communities with antecedent maximum stream temperatures observed in this study probably reflects a combination of these controls and highlights a need to consider different sources of thermal alteration associated with flow regulation within e-flow frameworks.

The strength of associations between abiotic indices and macroinvertebrate community responses typically improved when seasonal models were considered, with no thermal indices comprising the most highly correlated models. This is in contrast to research highlighting that comparable ecological variance could be explained by flow and stream temperature variability within some regulated systems (Jackson *et al.*, 2007; Rolls *et al.*, 2013). This study found that hydrological indices relating to the timing of extreme flows were of high ecological significance across both regulated and non-regulated sites. The timing of hydrological controls within regulated environments will have implications for the life-history traits of macroinvertebrates, such as univoltine species that may take longer to recover if extreme events occur during a sensitive part of their life cycle (e.g., Robinson, Uehlinger, & Monaghan, 2004). The ecological implications of the timing of hydrological extremes were observed within this study, which highlighted significant associations between several univariate ecological responses and abiotic indices, including fauna reproducing by laying isolated eggs on the riverbed being positively associated with minimum flows in July. This could be attributed to different reasons, including the resistance of such eggs to higher flows, or increased amounts of phytoplankton being flushed downstream, which may otherwise encrust eggs and prevent embryonic development (Bovill, Downes, & Lancaster, 2013); the latter is plausible given high productivity within the

reservoirs studied that results in large quantities of organic matter being deposited within the tailwaters (House, Beatson, Martin, & Bowles, 2015; White, Wilding, House, Beatson, & Martin, 2016).

4.4 | Study implications

The need to explore ecological responses to multiple environmental variables has been advocated to advance the development of future e-flow strategies (Olden & Naiman, 2010; Acreman *et al.*, 2014). Integrating flow and thermal regimes could underpin e-flow methodologies because they both respond profoundly to flow regulation (Ellis & Jones, 2014) and possess comparable forms of variability that have been found to exert unique ecological controls (Poff *et al.*, 1997; Olden & Naiman, 2010). In addition, such information can be measured over long-term periods at high temporal resolutions via data logging devices, while a comparatively lower amount of ecological information is often available from freshwater environments to quantify biotic responses to flow and thermal alterations (e.g. Solans & García de Jalón, 2016) and guide e-flow frameworks (Acreman *et al.*, 2014). Such limitations were recognized within this study, but a rigorous screening process of ecological data was necessary despite reducing the total number of samples available for analysis. Nevertheless, utilizing macroinvertebrate data collected by routine biomonitoring programs represents a powerful tool in assessing key drivers of ecosystem health over long-term periods (Vaughan & Ormerod, 2010), which even at coarser taxonomic resolutions (such as family-level data used within this study) can provide robust relationships between environmental conditions and ecological responses across multiple years (e.g., Monk, Wood, Hannah, & Wilson, 2008; Durance & Ormerod, 2009; Worrall *et al.*, 2014). The methods adopted within this study could be readily applied to river systems impacted by flow regulation worldwide. Establishing ecohydrological and ecothermal associations within regulated systems allows primary mechanisms driving biotic alterations to be quantified; while such information in non-regulated systems provides an understanding of key hydrological and stream temperature dependencies that lotic ecosystems require in more natural environments. Such information could guide future e-flow methodologies by targeting specific aspects of regulated systems that should be altered or preserved to mitigate alterations to instream biota, as well as how flow and stream temperature variability could be manipulated to rehabilitate or restore lotic ecosystems.

5 | CONCLUSIONS

Flow regulation alters various components of fluvial environments, including hydrological and stream temperature variability, which has been found to alter river ecosystems globally. This study explored the controls of flow and stream temperature variability on macroinvertebrate communities across paired regulated and non-regulated systems associated with three reservoirs. Thermal regimes were comparable between all sites (albeit with consistent differences in the magnitude of stream temperature variability), while regulated sites typically exhibited reduced low-flow variability and peak flows that regularly exceeded discharges at non-regulated sites. The functional

traits of macroinvertebrate communities responded significantly to flow regulation (specifically when biomonitoring indices were considered) but did not differ significantly between river catchments, while community abundances did not display such spatial consistency, highlighting contrasting taxonomic compositions between watercourses. As such, functional traits could provide reliable ecological information for guiding the implementation of regionally uniform e-flow methodologies. Macroinvertebrate communities responded significantly to various flow indices, particularly the timing of extreme flows, while stream temperature variability was not found to be a key driver of biotic change in this study. Currently, few studies have explored ecological responses to flow and thermal regimes within river systems and specifically regulated environments; thus, further research is required to unveil long-term ecological responses to changes in antecedent flow and stream temperature variability associated with impoundments. This could facilitate comparisons between key drivers of ecological variability within regulated (impact) and non-regulated (control) systems, which could go some way to informing e-flow frameworks on key ecosystem dependencies and drivers of biotic change associated with flow regulation.

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APPENDIX A

A. Introduction

The following appendix summarizes the procedure used to incorporate the input of specialist freshwater macroinvertebrate ecologists in the UK to refine the functional trait values used in this study. Due to the initial traits database being developed within France, this expert opinion approach was conducted to improve the relevance of trait values for UK taxa at the taxonomic resolution available for this study.

A. Methodology and analysis

Specialists across various academic and industrial institutions within the UK were consulted on the use of the traits database used within this study (Tachet *et al.*, 2010). The inputs of macroinvertebrate specialists were utilized within two broad categories. Firstly, generic comments were considered for procedures involved with processing functional traits. Secondly, specialists were asked to confirm, validate, and (where necessary) propose revisions to trait values (indicated by whether values should be increased or decreased) of taxa most sensitive to flow regulation within this study. Taxa most sensitive to flow regulation were identified across spring and autumn samples by conducting “Similarity Percentages” (SIMPER) analysis on $\ln(x + 1)$

TABLE A1 SIMPER outputs showing the most sensitive macroinvertebrate families to flow regulation across spring and autumn. The average contribution of each taxa towards the overall dissimilarity is displayed, alongside the average $\ln(x + 1)$ transformed abundance in non-regulated and regulated systems

Spring				Autumn			
Taxa	Overall dissimilarity	Average non-regulated	Average regulated	Taxa	Overall dissimilarity	Average non-regulated	Average regulated
Hydropsychidae	0.032	0.75	5.24	Hydropsychidae	0.041	1.35	6.49
Asellidae	0.029	0.30	4.38	Sphaeriidae	0.032	1.93	5.48
Heptageniidae	0.023	3.50	0.64	Asellidae	0.029	0.77	4.45
Sphaeriidae	0.022	1.93	4.23	Caenidae	0.023	0.34	3.23
Planariidae	0.022	0.84	3.56	Heptageniidae	0.023	3.44	0.69
Baetidae	0.019	5.32	3.10	Tipulidae	0.021	3.07	0.29
Lymnaeidae	0.019	0.00	2.64	Gyrinidae	0.019	0.34	2.77
Caenidae	0.018	0.51	2.96	Planariidae	0.019	0.59	2.66
Taeniopterygidae	0.018	2.51	0.00	Gammaridae	0.018	3.62	2.66
Erpobdellidae	0.016	0.29	2.40	Erpobdellidae	0.018	0.24	2.41

transformed taxonomic abundances (Table A1). The values of 82 traits (across 12 grouping features - see Table 2 and the main body of text for the nomenclature of functional traits) of these sensitive taxa were obtained by conducting a family-average (where all genus/species within the database were equally weighted) of standardized trait values (whereby all grouping features summed to 1) and subsequently multiplied by 100, with these values being sent to freshwater specialists. The influence of different family-average weighting techniques was assessed based on the 44 macroinvertebrate samples used within this study ("family-level" dataset herein). Three sets of family-average trait values were considered (a) equally weighted, (b) regionally weighted, and (c) nationally weighted. The initial processing of all three sets of trait values involved removing non-UK taxa from the database, as well as Chironomidae and taxa recorded at a taxonomic resolution coarser than family-level and values were subsequently standardized (as above). Equally weighted trait values were then calculated by averaging trait values across each macroinvertebrate family. Regionally weighted trait values were calculated based on the likelihood of sampling different taxa from river systems (both regulated and non-regulated) across the Somerset region. This was obtained from a dataset including 61 macroinvertebrate samples taken by the Environment Agency and Wessex Water (within both non-regulated and regulated systems) across Somerset ("species-level" dataset herein). Specimens were identified to genus or species level at a taxonomic resolution equal to or greater than that recorded within the traits database, with the exception of Cladocera, Collembola, Hydracarina, Microturbellaria, Nematomorpha, Nematoda, and Oligochaeta that were identified as such and excluded from subsequent analyses. Trait values were multiplied by the percentage of samples that each taxa was located within from the species-level dataset. Where all species within a specific family were absent from the species-level dataset, trait values were maintained (thus meaning they were equally weighted) and subsequent values were averaged across each family. A nationally weighted family average was calculated using the same procedure as before, only using species occurrence data taken as part of developing River Invertebrate Prediction and Classification System (Wright *et al.*, 1996) in place of the taxonomic percentage occurrences obtained in the species-level dataset.

Subsequently, the values from all three types of trait calculations were standardized (as above). A trait by taxonomic abundance array was then created by multiplying trait values by $\ln(x + 1)$ transformed taxonomic abundances, and each trait was averaged across all taxa and standardized (as above).

The reliability of calculating functional traits by weighting taxa by regional and national percentage occurrence datasets was assessed by subtracting each of these matrices by the equally weighted family average and reviewing how trait values responded (i.e., increased, decreased, or no change) compared to the suggestions proposed by macroinvertebrate specialists (Table B2). Non-metric multidimensional scaling (NMDS) was used to visualize differences of trait compositions outputted from the three different family-average weighting procedures using the "metaMDS" function and were statistically explored using a permutational multivariate analysis of variance (PERMANOVA) via the "adonis" function within the Vegan package.

A. Results

Macroinvertebrate specialists provided several comments, although only three were consistently reported. Firstly, experts commented on the general validity of trait values within a UK context, supporting the use of this traits database within this research. Secondly, specialists discouraged conducting averages for Chironomidae and Oligochaeta, due to high levels of species diversity within these taxonomic groups. As such, these taxa, along with any other taxa recorded at a taxonomic resolution coarser than family-level, were excluded from the traits procedure. Thirdly, specialists discussed how a family average based on equal weights may give more weight to rare species and less influence to common taxa within fluvial environments. This shaped the results

TABLE A2 Percentage of trait value alterations that matched between UK specialist moderations and different family averages based on different weighting procedures

	Regional	National
Correct	42.7	27.3
No change	39.2	42.0
Incorrect	18.2	30.8

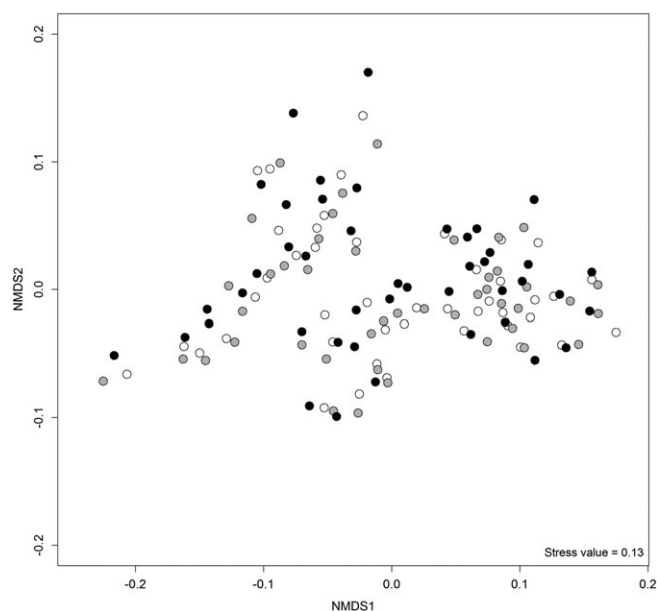


FIGURE A1 NMDS plot for functional trait compositions obtained from different family-averaged weighting procedures. White circles = equally weighted, gray circles = regionally weighted, black circles = nationally weighted

reported in the rest of this appendix based on different family-averaged weighting procedures.

Macroinvertebrate specialists proposed 143 alterations out of 1,066 trait values (13%), highlighting the congruency of the traits database with the opinions of UK specialists. Family-averaged trait values were in greater agreement with the moderations of expert opinions when the weighting of species was based on a regional likelihood of occurrence, compared those obtained from the River Invertebrate Prediction and Classification System national dataset (Table A2).

The NMDS procedure showed no discernible shifts in the multivariate location between the trait compositions obtained from

the different family-averaged weighting procedures (Figure A1), and PERMANOVA highlighted that these did not differ significantly ($F = 2.00$, p -value = 0.083).

The results highlight that family-average trait values based on a likelihood of occurrence obtained from regional biomonitoring practices improved the congruency between trait values and the opinions of macroinvertebrate specialists. However, no discernible changes in trait compositions could be obtained from weighting family averages differently, showing that all three types of trait family averages produced statistically comparable compositions.

APPENDIX B

B. Introduction

The following appendix displays statistical outputs from different analyses conducted within this study. It firstly reveals the full set of results obtained from permutational multivariate analysis of variance (PERMANOVA) processed in alternative forms from those included within the main body of text. Secondly, results are displayed from second-order polynomial regression analyses between a subset of flow and thermal indices and univariate macroinvertebrate responses.

B. Data analysis

This study conducted PERMANOVA to assess how four multivariate ecological responses (MERs—comprising different ecological information obtained from macroinvertebrate samples, details of these are described in the main body of text) responded to flow regulation, as well as spatial and temporal controls. The additive and interactive effects of “site position” (i.e., upstream—non-regulated and downstream—regulated sites), “reservoir” (i.e., separate river systems hosting each impoundment), “season,” and “year” were assessed via the “adonis” function within the Vegan package. In addition, a nested PERMANOVA was conducted to test for the influence of “site

TABLE B1 Results from PERMANOVA between different primary factors and MERs. Stars denote significant models: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$

Primary factor combinations	Taxonomic		Biological traits		All functional traits		Functional traits and biomonitoring indices	
	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value
Site position	0.36	0.001***	0.40	0.001***	0.40	0.001***	0.41	0.001***
Reservoir	0.06	0.026*	0.04	0.120	0.06	0.055	0.04	0.096
Season	0.04	0.140	0.02	0.395	0.02	0.395	0.02	0.388
Year	0.04	0.116	0.04	0.131	0.04	0.103	0.04	0.143
Site position:reservoir	0.03	0.046*	0.03	0.054	0.03	0.079	0.03	0.045*
Site position:season	0.01	0.31	0.01	0.603	0.01	0.578	0.01	0.625
Reservoir:season	0.01	0.848	0.01	0.5	0.01	0.592	0.01	0.525
Site position:year	0.01	0.25	0.01	0.375	0.01	0.415	0.01	0.468
Reservoir:year	0.03	0.042*	0.03	0.053	0.03	0.039*	0.03	0.039*
Season:year	0.01	0.657	0.01	0.57	0.01	0.649	0.01	0.605
Site position:reservoir:season	0.01	0.716	0.01	0.468	0.01	0.492	0.01	0.482
Site position:reservoir:year	0.02	0.277	0.01	0.339	0.01	0.33	0.01	0.356
Site position:season:year	0.01	0.513	0.01	0.381	0.01	0.464	0.01	0.395
Reservoir:season:year	0.01	0.671	0.01	0.572	0.01	0.508	0.01	0.606
Site position:								
Reservoir:season:year	0.02	0.207	0.02	0.191	0.02	0.171	0.02	0.206

(criteria for selecting these explanatory and response variables are summarized in the main body of text - see Figure 2). The p -values of these models are summarized within this appendix, with the model significance being determined by adjusting the significant α level via an alternative to the Bonferroni correction, which multiplies the model's degrees of freedom by 0.05 before dividing by the total number of tests.

(a)								
Univariate macroinvertebrate responses	QNCRR	QPORR	QCVANNMAX	QSEPMIN	QJUNMIN	QSTDMAXJW	QSTDMINJW	QJULMIN
Reproduction.3	NS	NS	NS	S	S	NS	NS	S
Feeding.4	NS	NS	NS	NS	NS	NS	NS	NS
Trophic.1	NS	NS	NS	S	S	NS	NS	S
Velocity.1	NS	NS	NS	S	S	NS	NS	S
Reproduction.4	NS	NS	NS	S	NS	NS	NS	NS
LIFE	NS	NS	NS	S	S	NS	S	S
ASPT	NS	NS	NS	S	S	NS	S	S
PSI	NS	NS	NS	S	S	NS	NS	S
Univariate macroinvertebrate responses	QMEPOS	QD35MAX50	QLPC	QD91MAX50	QMAXJW	QMEMAXJW	TDAYMAX91	TNERR
Reproduction.3	NS	NS	NS	NS	NS	NS	NS	NS
Feeding.4	NS	NS	NS	NS	NS	NS	NS	NS
Trophic.1	NS	NS	NS	NS	NS	NS	NS	NS
Velocity.1	NS	NS	NS	NS	NS	NS	S	NS
Reproduction.4	NS	NS	NS	NS	NS	NS	NS	NS
LIFE	NS	NS	NS	NS	NS	NS	NS	NS
ASPT	NS	NS	NS	NS	NS	NS	S	NS
PSI	NS	NS	NS	NS	NS	NS	NS	NS
(b)								
Univariate macroinvertebrate responses	QNCRR	QPORR	QCVANNMAX	QSEPMIN	QJUNMIN	QSTDMAXJW	QSTDMINJW	QJULMIN
Reproduction.3	NS	NS	NS	NS	NS	NS	NS	NS
Feeding.4	NS	NS	NS	NS	NS	NS	NS	NS
Trophic.1	NS	NS	NS	NS	NS	NS	NS	NS
Velocity.1	NS	NS	NS	NS	NS	NS	NS	NS
Reproduction.4	NS	NS	NS	NS	S	NS	S	NS
LIFE	NS	NS	NS	NS	NS	NS	NS	NS
ASPT	S	NS	NS	NS	NS	NS	NS	NS
PSI	S	NS	NS	NS	NS	NS	NS	NS
Univariate macroinvertebrate responses	QMEPOS	QD35MAX50	QLPC	QD91MAX50	QMAXJW	QMEMAXJW	TDAYMAX91	TNERR
Reproduction.3	NS	NS	NS	NS	NS	NS	NS	NS
Feeding.4	NS	NS	NS	NS	NS	NS	NS	NS
Trophic.1	NS	NS	NS	NS	NS	NS	NS	NS
Velocity.1	NS	NS	NS	NS	NS	NS	NS	NS
Reproduction.4	NS	NS	NS	S	NS	NS	S	NS
LIFE	NS	NS	NS	NS	NS	NS	NS	NS
ASPT	NS	NS	NS	NS	NS	NS	NS	NS
PSI	NS	NS	NS	NS	NS	NS	S	NS

TABLE C1 Flow and thermal indices used within this study. They are organized by which facet of the natural flow or thermal regime they predominantly correspond to

Flow indices.	Description	Thermal indices.	Description.
<i>Magnitude.</i>			
QMEAN	Mean average discharge	TMEAN	Mean average temperature
Q50	Median discharge	T50	Median temperature
QCVANN	Coefficient of variation of discharges	TCVANN	Coefficient of variation of temperature
QDFRANGE	Range of discharges	TDFRANGE	Range of temperatures
QMR	Mean annual runoff. $QMEAN \div \text{catchment area}$		
QJAN	Mean January discharge	TJAN	Mean January temperature
QFEB	Mean February discharge	TFEB	Mean February temperature
QMAR	Mean March discharge	TMAR	Mean March temperature
QAPR	Mean April discharge	TAPR	Mean April temperature
QMAY	Mean May discharge	TMAY	Mean May temperature
QJUN	Mean June discharge	TJUN	Mean June temperature
QJUL	Mean July discharge	TJUL	Mean July temperature
QAUG	Mean August discharge	TAUG	Mean August temperature
QSEP	Mean September discharge	TSEP	Mean September temperature
QOCT	Mean October discharge	TOCT	Mean October temperature
QNOV	Mean November discharge	TNOV	Mean November temperature
QDEC	Mean December discharge	TDEC	Mean December temperature
Q1	Discharge exceeded 1% of the time	T1	Temperature exceeded 1% of the time
Q5	Discharge exceeded 5% of the time	T5	Temperature exceeded 5% of the time
Q10	Discharge exceeded 10% of the time	T10	Temperature exceeded 10% of the time
Q20	Discharge exceeded 20% of the time	T20	Temperature exceeded 20% of the time
Q25	Discharge exceeded 25% of the time	T25	Temperature exceeded 25% of the time
Q75	Discharge exceeded 75% of the time	T75	Temperature exceeded 75% of the time
Q80	Discharge exceeded 80% of the time	T80	Temperature exceeded 80% of the time
Q90	Discharge exceeded 90% of the time	T90	Temperature exceeded 90% of the time
Q95	Discharge exceeded 95% of the time	T95	Temperature exceeded 95% of the time
Q99	Discharge exceeded 99% of the time	T99	Temperature exceeded 99% of the time
Q10Q90	Ratio of 10th and 90th discharge percentile. $Q10 \div Q90$	T10 T90	Ratio of 10th and 90th temperature percentile. $T10 \div T90$
Q20Q80	Ratio of 20th and 80th discharge percentile. $Q20 \div Q80$	T20 T80	Ratio of 20th and 80th temperature percentile. $T20 \div T80$
Q25Q75	Ratio of 25th and 75th discharge percentile. $Q25 \div Q75$	T25 T75	Ratio of 25th and 75th temperature percentile. $T25 \div T75$
Q1Q50	Ratio of 1st and 50th discharge percentile. $Q1 \div Q50$	T1 T50	Ratio of 1st and 50th temperature percentile. $T1 \div T50$
Q5Q50	Ratio of 5th and 50th discharge percentile. $Q5 \div Q50$	T5 T50	Ratio of 5th and 50th temperature percentile. $T5 \div T50$
Q10Q50	Ratio of 10th and 50th discharge percentile. $Q10 \div Q50$	T10 T50	Ratio of 10th and 50th temperature percentile. $T10 \div T50$
Q20Q50	Ratio of 20th and 50th discharge percentile. $Q20 \div Q50$	T20 T50	Ratio of 20th and 50th temperature percentile. $T20 \div T50$
Q25Q50	Ratio of 25th and 50th discharge percentile. $Q25 \div Q50$	T25 T50	Ratio of 25th and 50th temperature percentile. $T25 \div T50$
Q75Q50	Ratio of 75th and 50th discharge percentile. $Q75 \div Q50$	T75 T50	Ratio of 75th and 50th temperature percentile. $T75 \div T50$
Q80Q50	Ratio of 80th and 50th discharge percentile. $Q80 \div Q50$	T80 T50	Ratio of 80th and 50th temperature percentile. $T80 \div T50$
Q90Q50	Ratio of 90th and 50th discharge percentile. $Q90 \div Q50$	T90 T50	Ratio of 90th and 50th temperature percentile. $T90 \div T50$
Q95Q50	Ratio of 95th and 50th discharge percentile. $Q95 \div Q50$	T95 T50	Ratio of 95th and 50th temperature percentile. $T95 \div T50$
Q99Q50	Ratio of 99th and 50th discharge percentile. $Q99 \div Q50$	T99 T50	Ratio of 99th and 50th temperature percentile. $T99 \div T50$

(Continues)

TABLE C1 (Continued)

Flow indices.	Description	Thermal indices.	Description.
QS100	Range discharge variability. $QDFRANGE \div Q50$	TS100	Range temperature variability. $TDFRANGE \div T50$
QS50	Interquartile discharge variability. $(Q75-Q25) \div Q50$	TS50	Interquartile temperature variability. $(T75-T25) \div T50$
QS80	90th and 10th percentiles discharge variability $(Q90-Q10) \div Q50$	TS80	90th and 10th percentiles temperature variability $(T90-T10) \div T50$
QSK1	Discharge skewness one. $QMEAN \div Q50$	TSK1	Temperature skewness one. $TMEAN \div T50$
QSK2	Discharge skewness two. $(QMEAN-Q50) \div Q50$	TSK2	Temperature skewness two. $(TMEAN-T50) \div T50$
QSMED	Specific median discharge. $Q50 \div \text{Catchment area}$		
QSTDEV	Standard deviation of discharges	TSTDEV	Standard deviation of temperatures
QMAX	Maximum discharge	TMAX	Maximum temperature
QSMAX	Specific maximum discharge $QMAX \div \text{Catchment area}$		
QAMAX	Annual maximum discharge. $QMAX \div Q50$	TAMAX	Annual maximum temperature $TMAX \div T50$
QJANMAX	Maximum January discharge	TJANMAX	Maximum January temperature
QFEBMAX	Maximum February discharge	TFEBMAX	Maximum February temperature
QMARMAX	Maximum March discharge	TMARMAX	Maximum March temperature
QAPRMAX	Maximum April discharge	TAPRMAX	Maximum April temperature
QMAYMAX	Maximum May discharge	TMAYMAX	Maximum May temperature
QJUNMAX	Maximum June discharge	TJUNMAX	Maximum June temperature
QJULMAX	Maximum July discharge	TJULMAX	Maximum July temperature
QAUGMAX	Maximum August discharge	TAUGMAX	Maximum August temperature
QSEPMAX	Maximum September discharge	TSEPMAX	Maximum September temperature
QOCTMAX	Maximum October discharge	TOCTMAX	Maximum October temperature
QNOVMAX	Maximum November discharge	TNOVMAX	Maximum November temperature
QDECMAX	Maximum December discharge	TDECMAX	Maximum December temperature
QCVANNMAX	Coefficient of variation of monthly maximum discharge	TCVANNMAX	Coefficient of variation of monthly maximum temperature
QDFMEDMAX	Median maximum monthly discharge $\div Q50$	TDFMEDMAX	Median maximum monthly temperature $\div T50$
HQ	High discharge volume. Mean maximum monthly discharge $\div Q50$	HT	High temperature. Mean maximum monthly temperature $\div T50$
QMAX90	Maximum discharge for the previous 90 days	TMAX90	Maximum temperature for the previous 90 days
QMAX180	Maximum discharge for the previous 180 days	TMAX180	Maximum temperature for the previous 180 days
QMAX270	Maximum discharge for the previous 270 days	TMAX270	Maximum temperature for the previous 270 days
QMIN	Minimum discharge	TMIN	Minimum temperature
QJANMIN	Minimum January discharge	TJANMIN	Minimum January temperature
QFEBMIN	Minimum February discharge	TFEBMIN	Minimum February temperature
QMARMIN	Minimum March discharge	TMARMIN	Minimum March temperature
QAPRMIN	Minimum April discharge	TAPRMIN	Minimum April temperature
QMAYMIN	Minimum May discharge	TMAYMIN	Minimum May temperature
QJUNMIN	Minimum June discharge	TJUNMIN	Minimum June temperature
QJULMIN	Minimum July discharge	TJULMIN	Minimum July temperature
QAUGMIN	Minimum August discharge	TAUGMIN	Minimum August temperature
QSEPMIN	Minimum September discharge	TSEPMIN	Minimum September temperature
QOCTMIN	Minimum October discharge	TOCTMIN	Minimum October temperature
QNOVMIN	Minimum November discharge	TNOVMIN	Minimum November temperature
QDECMIN	Minimum December discharge	TDECMIN	Minimum December temperature
QCVANNMIN	Coefficient of variation of monthly minimum discharge	TCVANNMIN	Coefficient of variation of monthly minimum temperature
QSMIN	Specific minimum discharge. $QMIN \div \text{catchment area}$		
<i>Frequency.</i>			
QFRE1	Number of flow events greater than Q50	TFRE1	Number of temperature events greater than T50
QFRE3	Number of flow events greater than $3 \times Q50$	TFRE3	

(Continues)

TABLE C1 (Continued)

Flow indices.		Description	Thermal indices.		Description.
					Number of temperature events greater than three times T50
QHPC		High pulse count. Number of flow events greater than Q25	THPC		High pulse count. Number of temperature events greater than T25
QLPC		Low pulse count. Number of flow events less than Q75	TLPC		Low pulse count. Number of temperature events less than T75
<i>Duration</i>					
QDAYMAX35		Average 35-day (7 week) maximum discharge	TDAYMAX35		Average 35-day (7 week) maximum temperature
QDAYMAX91		Average 91-day (13 week) maximum discharge	TDAYMAX91		Average 91-day (13 week) maximum temperature
QDAY35MAX50		$QDAYMAX35 \div Q50$	TDAY35MAX50		$TDAYMAX35 \div T50$
QDAY91MAX50		$QDAYMAX91 \div Q50$	TDAY91MAX50		$TDAYMAX91 \div T50$
Q5MEAN		Monthly high flow duration index. $Q5 \div QMEAN$	T5MEAN		Monthly high temperature duration index. $T5 \div TMEAN$
QDAYMIN35		Average 35-day (7-week) minimum discharge	TDAYMIN35		Average 35-day (7-week) minimum temperature
QDAYMIN91		Average 91-day (13-week) minimum discharge	TDAYMIN91		Average 91-day (13-week) minimum temperature
QDAY35MIN50		$QDAYMIN35 \div Q50$	TDAY35MIN50		$TDAYMIN35 \div T50$
QDAY91MIN50		$QDAYMIN91 \div Q50$	TDAY91MIN50		$TDAYMIN91 \div T50$
Q95QMEAN		Monthly low flow duration index. $Q95 \div QMEAN$	T95TMEAN		Monthly low temperature duration index. $T95 \div TMEAN$
QZEROWEEK		Number of weeks possessing zero flow	TZEROWEEK		Number of weeks possessing frozen conditions
QZEROMON		Number of months possessing zero flow	TZEROMON		Number of months possessing frozen conditions
<i>Timing</i>					
QMAXJW		Julian week occurrence of the maximum discharge	TMAXJW		Julian week occurrence of the maximum temperature
QMEMAXJW		Mean average of the seven Julian weeks possessing the highest discharges	TMEMAXJW		Mean average of the seven Julian weeks possessing the highest temperatures
QSTDMAXJW		Standard deviation of the seven Julian weeks possessing the highest discharges	TSTDMAXJW		Standard deviation of the seven Julian weeks possessing the highest temperatures
QCV7JWMAX		Coefficient of variation of the seven Julian weeks possessing the highest discharges	TCV7JWMAX		Coefficient of variation of the seven Julian weeks possessing the highest temperatures
QMINJW		Julian week occurrence of the maximum discharge	TMINJW		Julian week occurrence of the maximum temperature
QMEMINJW		Mean average of the seven Julian weeks possessing the lowest discharges	TMEMINJW		Mean average of the seven Julian weeks possessing the lowest temperatures
QSTDMINJW		Standard deviation of the seven Julian weeks possessing the lowest discharges	TSTDMINJW		Standard deviation of the seven Julian weeks possessing the lowest temperatures
QCV7JWMIN		Coefficient of variation of the seven Julian weeks possessing the lowest discharges	TCV7JWMIN		Coefficient of variation of the seven Julian weeks possessing the lowest temperatures
<i>Rate of change</i>					
QMEPOS		Mean average positive change between flow conditions. Mean positive changes between flow coinweek 5	TMEPOS		Mean average positive change between temperature conditions. Mean positive changes between flow coinweek 5
QMENEG		Mean average negative change between flow conditions. Mean positive changes between flow coinweek 5	TMENEG		Mean average negative change between temperature conditions. Mean positive changes between flow coinweek 5
QMEDIFF		Mean average difference between positive and negative changes in flow conditions	TMEDIFF		Mean average difference between positive and negative changes in temperature conditions
QNCRR		Number of weeks with constant discharge between weeks	TNCRR		Number of weeks with a constant temperature between weeks
QNERR		Number of negative changes in flow conditions	TNERR		Number of negative changes in temperature conditions
QPORR		Number of positive changes in flow conditions	TPORR		Number of positive changes in temperature conditions
QSTDDIFF		Standard deviation of the difference between positive and negative changes in flow conditions	TSTDDIFF		Standard deviation of the difference between positive and negative changes in temperature conditions

B. Results

The PERMANOVA highlighted that the inclusion of interaction terms did not improve the variance explained by different environmental

controls and few of these models differed significantly (Table B1). In addition, a nested PERMANOVA revealed statistically identical outputs to those produced by a non-nested design, using “site position” as a primary factor (see the first row in Table B1).

Second-order polynomial regression analysis highlighted that more statistically significant associations existed between individual macroinvertebrate responses and abiotic indices within regulated systems ($n = 23$; Table B2a), relative to non-regulated samples ($n = 7$; Table B2b).

APPENDIX C

The following appendix provides details of the definitions for all flow (discharge) and thermal indices processed in this study (Table C1).